The Functional Morphology of *Lyonsia californica* Conrad, 1837

(Bivalvia)

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(7 Text figures)

INTRODUCTION

THE FAMILY LYONSIIDAE comprises 3 genera: *Lyonsia, Mytilimeria* and *Entodesma* (ABBOTT, 1954, p. 468). The last is considered by THIELE (1963, p. 936) as a subgenus of *Lyonsia*. Species of *Lyonsia* are widely distributed in the northern hemisphere including the west coast of Europe and the Atlantic and Pacific coasts of North America.

Lyonsia californica CONRAD, 1837, occurs on the Pacific coast of North America from Puget Sound to Lower California (ABBOTT, 1954, p. 468). According to KEEN (1937, p. 21) it ranges from 24° to 56° North Latitude. Isolated references to this species were found in the papers of ATKINS (1937), KELLOGG (1915) and YONGE (1952), but there is no special research dealing with all aspects of the functional morphology of this species.

This paper is concerned with observations on the structure, ciliary currents of feeding and digestion, and other functional adaptations of *Lyonsia californica*. The animals were collected at Lawson's Flat and White Gulch in Tomales Bay, Marin County, California; the observations on live specimens were made at Pacific Marine Station, Dillon Beach, California.

SHELL

The shell is about 3 times as long as it is broad and moderately obese in the anterior part where the shell valves are rounded, while the posterior end is laterally compressed. It is thin, fragile and almost transparent. The umbo is situated approximately one-third from the anterior end; the beak area is swollen. The shell is made largely of nacreous material and fractures easily. BOGGILD (1930, p. 291) noted that the shell valves consisted of a nacreous substance between two layers of fine prismatic structure.

The valves are covered by a thick layer of periostracum which covers the margin of the shell; weak, radial, dark lines run through the periostracum. Dorsally the two shell valves are joined along their entire length by periostracum; it covers the base of the siphons and the ventral surface of the fused mantle edges. This feature is considered as primitive by YONGE (1952, p. 446). In the living animal sand grains are found attached everywhere on the shell but adhere more firmly at the base of the siphons and to the ventral periostracum as in *Entodesma saxicola* BAIRD, 1863 (YONGE, 1952, p. 440). The dense accumulation of sand grains around the base of the siphons fills the posterior gape when the siphons are withdrawn.

There is a lithodesma under the hinge attached to the ligament which is very similar to that of *Entodesma saxicola* (YONGE, 1952, p. 446).

The margins of both valves are poorly calcified in the siphonal region as in *Pandora inaequivalvis* (LINNAEUS, 1758) (ALLEN, 1954, p. 474). The valves are slightly inaequivalve. When closed, the periostracum of the free margin of the left valve folds over and fits against the outer marginal region of the right valve.

The shell of the largest animal encountered in this study measured 38 mm in length, 16 mm in height and 12 mm in width.

MANTLE

The mantle edges and periostracal grooves are fused ventrally (Figure 1, mef). There is a pedal gape (pg) and a smaller pallial aperture (a_1), which opens about 5 mm from the base of the inhalant siphon (in). The fourth aperture in *Lutraria* and *Thracia* lies closer to the inhalant siphon than in *Lyonsia californica* and in *Entodesma saxicola* (ATKINS, 1937, p. 444). According to KELLOGG's figures of *E. saxicola* and *Mytilimeria nuttallii*

Conrad, 1837 (1915, p. 654; figs. 22, 26, 27, 28) the fourth aperture of the mantle is just posterior to the region in which the rejecta brought by the mantle currents collect. While Kellogg (*op. cit.*, p. 656) did not note the significance of this opening, Yonge (1952, p. 447) thought that it was a purely structural feature, possibly a result of the manner in which the mantle edges fuse during development.
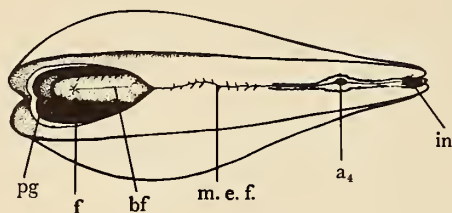

Figure 1

Lyonsia californica Conrad

ventral aspect of the animal, showing the pedal gape and foot with byssal groove and the fourth aperture

a₄ – 4th aperture   bf – byssus fold   f – foot
in – inhalant siphon   mef – mantle edges fused
pg – pedal gape

On both sides of the fourth aperture fusion is complete. The muscles cross the ventral region from one lobe to the other. In *Ensis siliqua* and *E. arcuatus* actual tissue fusion occurs only posteriorly to the fourth aperture (Atkins, 1937, p. 431). *Thracia villosiuscula* has a fourth aperture near the posterior end of the animal just below the inhalant siphon and exhibits a true tissue fusion (Atkins, *op. cit.*, p. 431).

SIPHONS

The siphons are transparent, separated and short (Figure 2). The basal region is covered with periostracum in which sand grains are incorporated. The cavity of the basal region represents a posterior extension of the mantle cavity (Yonge, 1952, p. 441). The base of each siphon is surrounded with many small tentacles. The aperture of the inhalant siphon is fringed with 9 simple tentacles. The exhalant siphon consists of a tapering tubular membrane without any tentacles between the aperture and the common outer ring. This arrangement is similar to that in *Lyonsia hyalina* as described by Morse (1919, p. 161).

Regularly distributed black spots are found on both siphons; on the exhalant siphon the spots are concen-

trated in the lower part, forming a dark ring. Many spots are present on the tentacles of the inhalant siphon.

As in *Pandora,* the siphons are not capable of great extension, and for this reason the animal is more or less
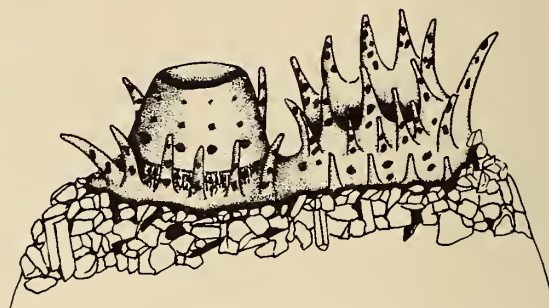

Figure 2
Appearance of fully extended siphons
projecting out of the shell valves

limited to the epifaunal regions of the substrate (Boss & Merrill, 1965, p. 183).

As in *Glossus humanus* (Linnaeus, 1758) specimens placed in a dish withdrew their siphons when a hand was placed lightly on the table on which the jar stood; this sensitivity is evidence that the animal normally inhabits quiet waters (Owen, 1953, p. 92). The exhalant siphon contracts by lateral constriction of its sides forming a figure 8 when seen from above; this is followed by the infolding of the siphonal edges.

THE MANTLE CAVITY

The disposition of the organs in the mantle cavity (Figure 3) is revealed after removal of the left shell valve and mantle lobe. The slightly smaller anterior adductor muscle (aam) and the larger posterior adductor muscle (pam) are situated in a line parallel with the dorsal margin. The important features of the different organs will be outlined below.

THE CTENIDIA

The outer demibranch consists only of a direct lamella, which is upturned and attached near the dorsal surface (Figure 3). The inner demibranch is broad and reflected. Ridewood (1903, p. 150), Kellogg (1915, p. 656) and Atkins (1937, p. 351) noted that in allied species the same phenomenon occurs. The lamellae are deeply pli-
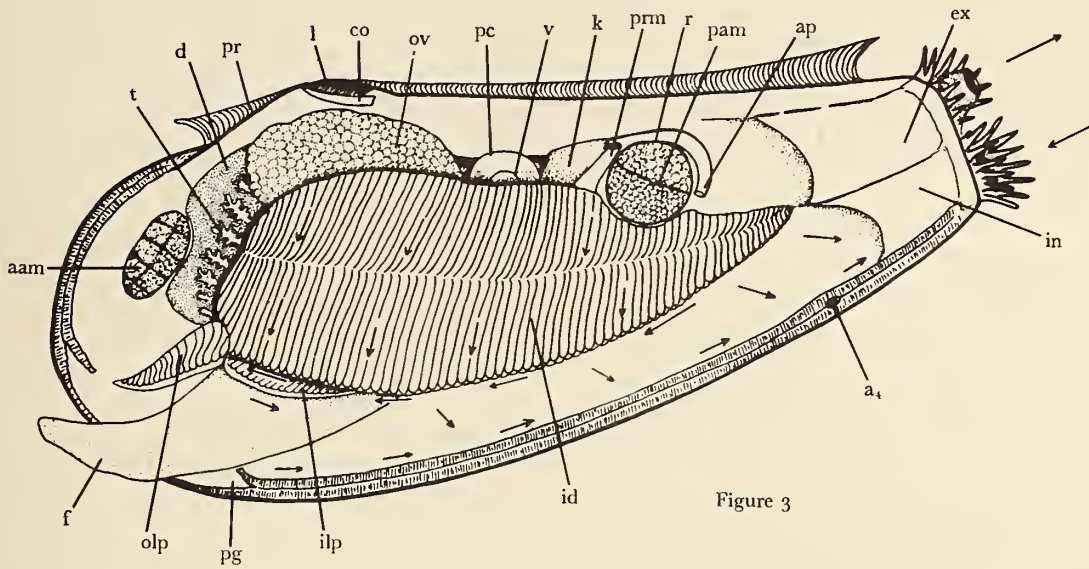
Figure 3

Figure 3

Lyonsia californica CONRAD

mantle cavity viewed from left side after removal of the left shell
valve and mantle lobe

a₄ – 4ᵗʰ aperture	aam – anterior adductor muscle	
ap – anal papilla co – lithodesma d – digestive diverticula	l – ligament olp – outer labial palp ov – ovary	
ex – exhalant siphon f – foot id – inner demibranch	pam – posterior adductor muscle pc – pericardium	
ilp – inner labial palp in – inhalant siphon k – kidney	pg – pedal gape pr – periostracum r – rectum	
	prm – posterior retractor muscle t – testis v – ventricle	
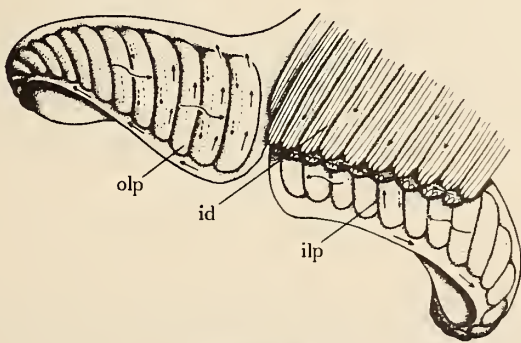
Figure 4

The labial palps of the left side. Shell length 19 mm

aam – anterior adductor muscle   id – inner demibranch
ilp – inner labial palp   olp – outer labial palp

eated and heterorhabdic. As in *Lyonsia norwegica*, 13 to 17 filaments form a plica, while the apical 5 are more strongly developed than the others. As with the remaining filaments, the apical filaments have a middle tract of long, coarse frontal cilia, bordered on each filament by tracts of fine, short cilia.

At the free edge of the inner demibranch there is a deep marginal groove (Figure 4). Ciliary currents were studied by the application of carmine, aquadag, and fine carborundum in minute quantities. The ctenidia are similar to those of *Lyonsia norwegica* (ATKINS, 1937, p. 350), *Mytilimeria nuttallii* (KELLOGG, 1915, p. 656) and *Entodesma saxicola* (KELLOGG, *op. cit.*, p. 659) and fall into ATKINS' Type E (ATKINS, *op. cit.*, p. 409).

Ciliary currents move downward to the margin of the outer demibranch and continue in the same direction on

the descending lamellae of the inner demibranch to its margin. On the two exposed faces of the ctenidium, particles are driven ventrally, therefore, while on the inner lamella of the inner demibranch, the movements of the particles are also ventral.

Along the marginal groove there is an oral current moving material on the ventral margin of the inner demibranch to be taken on the palp folds and passed to the mouth (Figure 4).

The ciliary mechanism on the ctenidia of *Lyonsia californica* is similar to that of *L. norwegica,* described by ATKINS (1937, p. 347).

Frontal cilia extend around the ventral ends of the filaments; they occur on both sides of each filament and beat toward the axial groove.

Latero-frontal cilia (10μ in length) are situated on a slight ridge. The lateral cilia are very similar to those of *Lyonsia norwegica.*

With the ctenidium deeply plicated, the marginal food groove has scalloped sides. The marginal groove in *Lyonsia californica* is deep and similar to that of *L. norwegica* described by ATKINS (*op. cit.,* p. 350).

Fine particles reach the principal filaments and adjacent filaments within the plical grooves. The principal filaments end at the bottom of the marginal groove. Particles carried in the principal filaments and the adjacent filaments come to the same deep channel.

Coarse particles are kept from entering the narrow interplical space and are carried on the plical crests or passed directly off the ctenidia, or are passed toward the mouth to fall on the mantle where they are removed.

The animal could contract the ctenidia, covering the principal filaments, and thus exposing a reduced surface to the current being directed to the mouth.

The ventral tips of the anterior filaments of the inner demibranch are inserted and fused to a distal oral groove and fall in Category II of the association of ctenidia and labial palps (STASEK, 1963, p. 91).

THE LABIAL PALPS

The labial palps are large, active and continually coiling. Each palp lamella bears 20 ridges on the inner surface. The inner demibranch of the ctenidium projects deeply between the palps. Particles form a narrow stream that moves in the oral groove, and are subjected to selection by the folds of the palps, eventually passing over them to the mouth. If material is not removed, it continues forward and is carried into the proximal oral groove.

Material bound in mucus which passed to the palp from the inner demibranch was rapidly transported anteriorly

and ventrally, being rejected at the free ventral margin of the palp.

The following ciliary currents may be recognized:
(a) On the floor of the groove between adjacent folds, particles are driven to the ventral border of the palp and from there moved to the tip of the palp where they are rejected (Figure 5 a, 5 b).
(b) On the crests of the folds and on the superficial slopes, particles are carried forward from fold to fold toward the mouth (Figure 5 a, 5 b).
(c) On the crests of the folds toward the dorsal border of the palp, particles are moved to the dorsal part of the labial palp where they form a resorting current.

In *Lyonsia californica* there is one main acceptance current, one rejection current and one dorsally directed resorting current (Figure 5).

Under normal conditions particles of carmine and carborundum are carried rapidly forward and downward over the folds, traveling over the folds without being
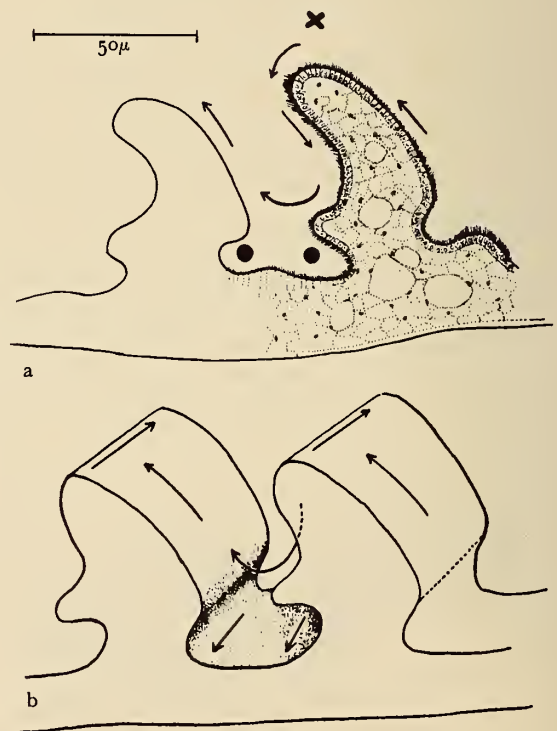

Figure 5

a – Section of the labial palps; ● indicates the position of a proximal current; x indicates the position of a distal current; arrows show the direction of an oral current
b – Diagrammatic representation of the ciliary mechanisms on the folded surface of the labial palps

deflected dorsally by the resorting current. However, some are taken on the crests of the ridges and transported dorsally by the dorsal resorting current. Particles are accumulated at the base of the palp and, with particles from the ctenidial margin, are passed into the lateral oral groove, then to the mouth where they are ingested.

Very few particles were carried in the deepest part of the grooves to be rejected by the free ventral border of the palp, as observed in *Petricola pholadiformis* LaMARCK, 1818 (PURCHON, 1955, p. 264).

THE VISCERAL MASS AND THE FOOT

The visceral mass of *Lyonsia californica* is very similar to that of *L. norwegica,* as described by PELSENEER (1891, p. 210). The digestive diverticula are placed anteriorly and ventrally, with the kidney posterior to the pericardium. This species is hermaphroditic, possessing two large pairs of gonads each with its own duct. The ovary occupies the dorsal region of the visceral mass and is surrounded by the testis which fills the ventral region of the digestive diverticula. Observations were made during the process of spawning, which occurred in April. Great numbers of eggs left the exhalant siphon followed in the same animal by a discharge of sperm. This alternation between the discharge of eggs and sperm continued for a few minutes. Fertilization occurs in the sea water as in *Entodesma saxicola* and *Mytilimeria nuttallii* (YONGE, 1952, p. 443).

The foot is slender, and, when fully distended, is half the length of the shell. There is a well developed byssus gland with a groove extending along the ventral side of the foot almost to its tip. The construction of byssus threads by adult animals was observed in the laboratory. YONGE (1952, p. 446) states that the foot and pedal gape are small in *Lyonsia norwegica. Lyonsia californica* is capable of burrowing. A specimen 20 mm long was observed to bury itself in 25 minutes. Once buried, the animal remains in the same position for a long time, which is indicated by the algal growth on the posterior end of the shell valves.

MUSCULATURE

The anterior adductor muscle of *Lyonsia californica* is smaller than the posterior adductor muscle, and both are located on the antero-posterior axis of the body.

The anterior pedal retractor muscle arises a short distance posterior to the anterior adductor, is poorly developed and its fibers spread out immediately below the epidermis on the antero-dorsal surface of the visceral mass.

The posterior retractor muscle arises anteriorly to the posterior adductor muscle, is well developed and inserts at the postero-dorsal part of the visceral mass.

Transverse muscle fibers arise in the epithelium of the visceral mass and pass inward either to the walls of the alimentary canal or transversely across the visceral mass to the opposite side.

THE ALIMENTARY CANAL
GENERAL STRUCTURE

The alimentary canal (Figure 6) was dissected from specimens that had been relaxed with magnesium chloride and preserved in alcohol. The internal structures of the stomach were studied in living animals. The stomach was
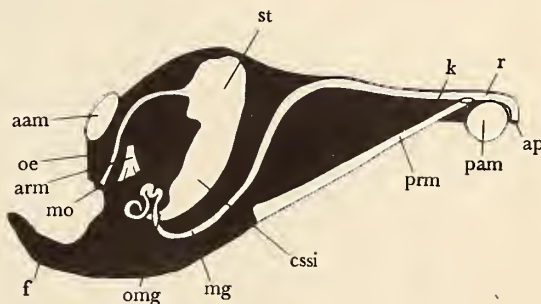
Figure 6

General dissection of the alimentary canal
ap – anal papilla   arm – anterior retractor muscle
cssi – combined style sac and mid-gut   f – foot   k – kidney
mg – mid gut   mo – mouth   oe – oesophagus
   omg – origin of the mid-gut at the base of the style sac
pam – posterior adductor muscle   r – rectum
   prm – posterior retractor muscle   st – stomach

opened by a mid-dorsal incision through the roof, and the right side of the stomach was drawn downward (Figure 7). The ciliary currents were investigated with the aid of carmine, aquadag and fine carborundum particles. The nomenclature used by GRAHAM (1949), OWEN (1953), PURCHON (1955) and REID (1965) has been followed.

The mouth (mo) opens into a long oesophagus (oe) that enters at the anterior part of the stomach (st). The lumen of the oesophagus is dorso-ventrally compressed. The stomach consists of two parts: a globular anterior region and a posterior elongated region. The combined
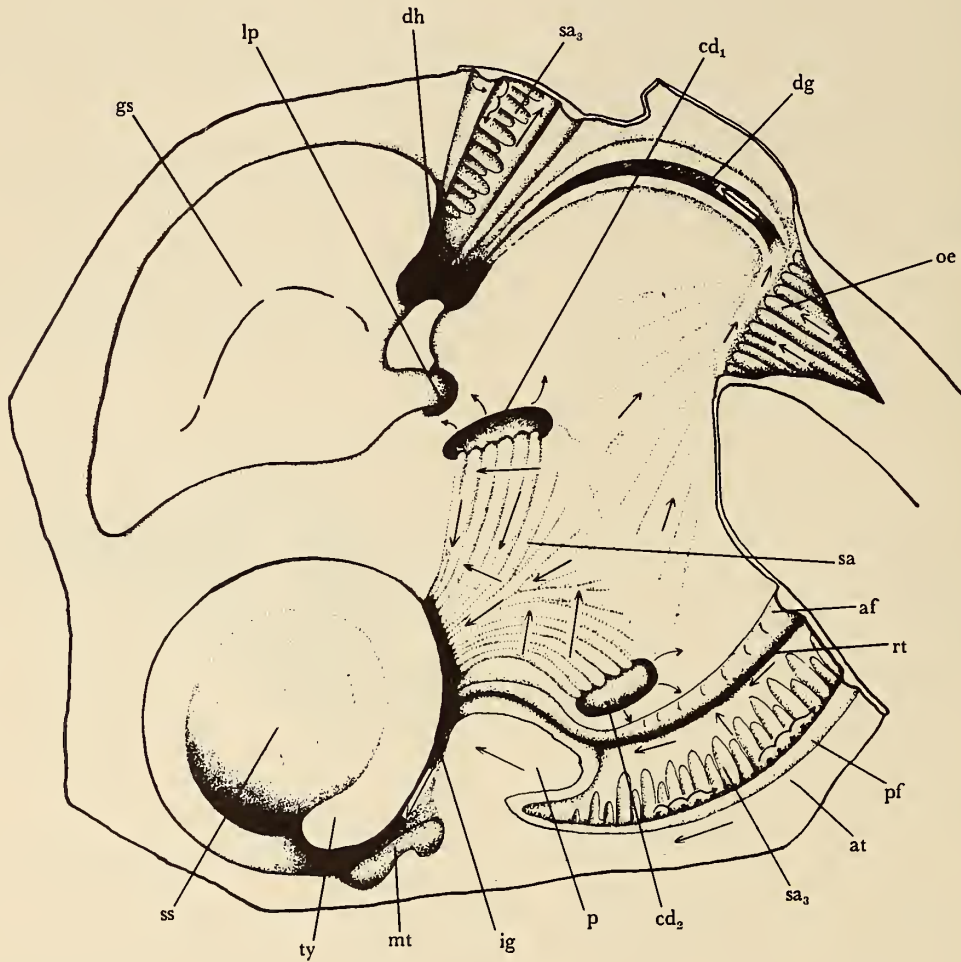
Figure 7

The interior of the stomach, seen from the right side, after opening
by making an incision in the right wall

af – anterior fold   at – acceptance tract   oe – oesophagus   p – ciliated pad   pf – posterior fold
cd₁ – left collecting duct   cd₂ – right collecting duct   rt – rejection tract   sa – sorting area
dg – dorsal groove   dh – dorsal hood   gs – gastric shield   sa₃ – posterior sorting area   ss – style sac
ig – intestinal groove   lp – left pouch   mt – minor typhlosole   ty – major typhlosole

style-sac and intestine open into the posterior and ventral region of the stomach. The intestine is convoluted in the region anterior to the stomach and then passes backward, proceeding posteriorly and dorsally over the kidney and the posterior adductor muscle to open at the anus.

STRUCTURE OF THE STOMACH

Lyonsia californica has a stomach of Type 4 as defined by PURCHON (1958, p. 488). The minor typhlosole (mt) ends where the anterior globular part of the stomach begins, so that the intestinal groove (ig) running across the floor of this region has no fold along it on the right side, though its left margin is bordered by the extension of the major typhlosole (ty). The major typhlosole is thick, large, and extends across the opening of the mid-gut to come in contact with the minor typhlosole. As in other bivalves which have stomach Type 4, the major typhlosole and the intestinal groove pass forward over the floor of the stomach, curving gradually to the left. The major typhlosole does not possess a tongue, nor does it enter any of the orifices of the ducts from the digestive diverticula on the anterior right side of the stomach (PURCHON, 1958, p. 489).

The dorsal hood (dh) is large and directed anteriorly to the left. It opens posteriorly on the left wall of the stomach and arches forward above the oesophagus and opens into the stomach anteriorly. The ventral wall of the stomach is covered with a finely ridged sorting area, posteriorly bordering on the intestinal groove which disappears, on the right side of the major typhlosole, into the intestine. The sorting area is composed of a regular series of alternately long and short folds, separated from one another by grooves with diverse ciliary currents setting up a sorting mechanism. The posterior sorting area (sa₃), which forms a Type A sorting mechanism (REID, 1965, p. 159), is well developed, extending dorsally over the right wall of the stomach and on to the right wall of the dorsal hood. The posterior margin of the sorting area is formed by a well developed fold (pf), while the anterior margin is bounded by the rejection ciliary tract (rt) which empties into the intestinal groove (ig) on the floor of the stomach at the point where the minor typhlosole ends. The anterior margin of the rejection tract is formed by a second fold with several small parallel ridges (af).

The gastric shield (gs) is well developed and attached to the left wall of the stomach by the teeth extending into the apertures of the left pouch (lp) and the dorsal hood. The left pouch is a blind hollow into which the anterior border of the gastric shield fits. This is similar to *Pandora*

inaequivalvis (PURCHON, 1958, p. 509). The left pouch of the Lyonsiidae falls into Section III, Group B of DINAMANI (1967, p. 262).

In the ventral part of the stomach wall there is a fan-shaped sorting area (sa), with a series of folds and ridges that have the same arrangement as the posterior sorting area, and drains particles into the intestinal groove. This well developed area extending from the mid-gut penetrates the two large apertures, one on the left anterior wall and the other on the right anterior wall. A similar condition exists in *Pandora*. The aperture of the left wall of the stomach was termed by ALLEN the "left caecum." In *Lyonsia californica* there are 17 to 20 folds, while in *P. inaequivalvis* there are 10 to 15. ALLEN (1954, p. 480) described this region as the "lateral rejection grooves." All ducts of the digestive diverticula open into the two larger apertures. Dissection of the main collecting ducts (cd) revealed the apertures of the ducts which open into them. Five ducts from the digestive diverticula open into the left aperture and 3 of them open into the right aperture of the stomach.

Particles accepted by the palps are carried through the oesophagus and carried to the roof of the stomach by the dorsal groove (dg), where they are caught by the tip of the crystalline style and directed to the posterior sorting area by its revolving action. The crystalline style in *Lyonsia californica* is large (7 mm long in a specimen of 19 mm overall length) and rotates in a clockwise direction when viewed from above. The particles in the posterior sorting area are directed against the ridges of the anterior fold. From here they are carried by the revolving style to the ridged surface of the posterior sorting area, where heavier particles are carried by the cilia of the grooves to the rejection tract (rt) and to the mid-gut by the intestinal groove (ig). The finer particles are conveyed dorsally from crest to crest across the ridges. Only the lighter particles are retained in the distal region of the dorsal hood, where they are included in the mass at the tip of the crystalline style. The acceptance tract (at) conveys particles along the roof of the dorsal hood and over the posterior wall of the stomach to the mid-gut.

The ciliary currents of the dorsal region convey fine particles from the tip of the style to the acceptance tract. Particles in the sorting area (sa) are conveyed in the grooves, by cilia, to the intestinal groove. Cilia on the crests of the folds beat from the right to the left, carrying particles to the left region of the stomach. Here, coarse particles are rejected in the grooves, while fine material passes across this region on the crests of adjacent ridges by ciliary action.

Particles that do not enter the digestive ducts are carried towards the oesophageal region of the stomach

where they join others that come from the oesophagus, and then both are carried to the base of the dorsal hood by the dorsal groove. The dorsal groove was noted by ALLEN (1948, p. 480), but not by PURCHON (1959, p. 509) in *Pandora inaequivalvis*.

The stomach of *Lyonsia californica* is similar to that of *Pandora inaequivalvis*. The single duct from the digestive diverticula which ALLEN (1954) established as entering the middle of the floor of the stomach and which he erroneously interpreted as "right caecum" (PURCHON, 1958, p. 508), and not seen by PURCHON in the same species, is not present in *Lyonsia californica*.

DISCUSSION

Lyonsia californica is adapted to live in a substratum of soft mud, and is found on muddy beaches. Algal growth confined to the siphonal region indicates that the animal buries itself in such a way that only the posterior part of the shell and siphons are exposed. The siphons are sensitive, and it is not probable that large quantities of material are normally taken into the pallial cavity. The siphons are short and never extend more than a few millimeters beyond the end of the shell.

The species has a well developed foot used to dig, and to orientate the animal when it digs.

The animal lives in quiet waters with little disturbance of the bottom deposits so that the water contains little suspended material. The presence of well developed sorting areas in the stomach is evidently desirable to reject large particles or excessive quantities of small particles (PURCHON, 1960, p. 487).

The stomach is very similar to that of *Pandora inaequivalvis*, which was studied by ALLEN (1954) and PURCHON (1958). In *Lyonsia californica* there is no simple duct from the digestive diverticula that PURCHON named DDD₃ and which ALLEN (1954, p. 480) interpreted as the right caecum and established as entering the floor of the stomach and communicating with the intestinal groove by a special groove. PURCHON (*op. cit.,* p. 508) was unable to find this duct in the animals that he studied but he inserted it later, as he said, in the figure of the stomach of *P. inaequivalvis*.

In *Lyonsia californica* the major typhlosole accompanied by the intestinal groove passes toward the openings of the collecting ducts and curves across the opening of the mid-gut to come into contact with the minor typhlosole. PURCHON believed that in *Pandora inaequivalvis* the major typhlosole and the intestinal groove terminate at the posterior border of the mouth of the collecting duct, which is situated on the left anterior wall of the stomach.

As PURCHON found in *Pandora inaequivalvis*, the digestive diverticula do not open into the left pouch.

A groove on the roof of the stomach and in which cilia beat backward and convey particles toward the dorsal hood, exists in *Lyonsia californica*, and this was also found in *Pandora inaequivalvis* by ALLEN. It was not seen by PURCHON when he studied the same species of *Pandora*.

The stomach of *Lyonsia californica* resembles in general the stomach of *Anodonta cygnea* (GRAHAM, 1949, p. 745), but is much more similar to that of *Pandora inaequivalvis*.

PURCHON (1958, p. 488 and 1960, p. 432) made an intensive study of the stomach in Bivalvia and found in 22 families the stomach that he defined as Number 4. The family Lyonsiidae is now the 23ʳᴰ family known to have this type of stomach.

Of 4 families in the super-family Pandoracea of the sub-order of Anomalodesmacea (ABBOTT, 1954, p. 468) we know that 2 have stomach type Number 4, Pandoridae and now Lyonsiidae. Future studies will prove if in the remaining 2 families, Periplomatidae and Thraciidae, the stomachs are of the same type as defined by PURCHON, proving that the form of the stomach is an indication of the phylogeny of the bivalves and not a consequence of the adaptations to different environments.

SUMMARY

Lyonsia californica CONRAD occurs in muddy substrates on the Pacific coast of North America from Puget Sound to Lower California. The calcareous shell is thin and largely nacreous. The periostracum is very thick and sand grains adhere to it. A lithodesma is present and dorsally the shell valves are united by the periostracum. The mantle edges are fused except in the region of the small fourth pallial aperture and along the relatively well developed pedal gape.

The anatomy and functioning of the stomach is described in detail. It belongs to type Number 4 as defined by PURCHON (1958, p. 488). The stomach of *Lyonsia californica* is similar to that of *Pandora inaequivalvis*.

ACKNOWLEDGMENTS

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